A REVISION OF THE LAKE VICTORIA

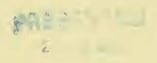
HAPLOCHROMIS SPECIES (PISCES, CICHLIDAE)

PART I: H. OBLIQUIDENS HILGEND.,
H. NIGRICANS (BLGR.),
H. NUCHISQUAMULATUS (HILGEND.)
AND H. LIVIDUS, SP. N.



P. H. GREENWOOD

East African Fisheries Research Organization, Jinja, Uganda.



Pp. 223-244; 2 Text-figs.

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 4 No. 5

LONDON: 1956

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), instituted in 1949, is issued in five series corresponding to the Departments of the Museum, and an Historical Series.

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 4, No. 5 of the Zoological series.

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

A REVISION OF THE LAKE VICTORIA HAPLOCHROMIS SPECIES (PISCES, CICHLIDAE)

PART I: H. OBLIQUIDENS HILGEND., H. NIGRICANS (BLGR.), H. NUCHISQUAMULATUS (HILGEND.)

AND H. LIVIDUS, SP. N.

By P. H. GREENWOOD.

CONTENTS

				,	ON	TEN	1.2						
INTRODUCTION	J												Page
Haplochr	mis oblia	· widone l	· Uilaan	.1	•	•	•	•					226
Syno	nymy an	d decemi	ntice	a.	•	•		•					226
Distr	nymy an	u descri	ption	•	•		•						227
Ecolo	ibution	•		•	•	•							229
Affin	ogy . ities and	tavanar				•	. •	•					229
Stud	v materia	l and di	atair	itus (or the	e spec	cies	•					230
orau,	y materia	a and di	stribu	tion	recor	ds	•						232
Haplochro	mic linid	46 CD D											
Syno	nymy and	d dossai	JV.	•	•	•	•		•				232
Distr	ibution				•								232
	gy .					•							234
	osis .	•											234
Study	materia	Innd di	• •		•	•	•						236
orday	materia materia	and di	stribu	tion 1	recor	ds							237
Haplochro	mic miavi	caus /DI											
Synor	nymy and	dens (DI	gr.)	•	•		•						237
Distri	bution					•							237
Ecolo	mar.	•	•	•		•		•		•			239
Diagr	gy .	•	•	•		•							239
Study	osis . material	Lama 41			•	. •							240
Study	materia	and dis	stribui	tion i	ecor	ds	•				٠		240
Hablachyo	mic marali												
Haplochro	mis muchi	squamu	atus (Hilge	end.)		•					٠.	241
Distri	ymy and bution								-				241
						•							242
Diam		• •	•		•		•						242
			, .		•								242
Othay	mate r ial	and dis	tribut	ion r	ecore	is	•						243
SUMMARY .													
	•				•		•						243
Acknowledgm	ENTC												1.5
REFERENCES .	E1419		•		•	•		•					243
		٠.	•		•	•	•						243
200L. 4, 5.													

INTRODUCTION

The species described in this paper form a well-defined ecological group within the *Haplochromis* species flock of Lake Victoria. All feed principally by grazing on epiphytic and epilithic algae.

As a group and severally they show obvious morphological adaptations to this particular feeding habit. Adaptation is most clearly seen in tooth-form and arrangement, which depart from those common to the majority of *Haplochromis* species.

Several other ecologico-morphological groups have evolved in Lake Victoria. Their existence raises questions regarding the possibility of providing a realistic basis for subdividing the present phylogenetically amorphous arrangement of the species.

There are, however, certain difficulties inherent in this procedure. A strictly morphological approach to sub-division is unworkable. Intergradation, rather than discreteness, of morphological group-characters might be said to typify this species flock. Such a situation is, however, not unexpected in a large group of oligophyletic origin which has undergone intense adaptive radiation during a short period of geological time (Regan, 1922; Greenwood, 1951).

Also, although some morphologically distinct species-complexes occupy equally distinctive ecological niches, there are other morphologically-homogeneous groups which cut across any attempted ecological classification.

Furthermore, in any ecologically-defined group there are grades of anatomical specialization such that the most and least specialized species are only with difficulty included in a supra-specific category defined by morphological criteria alone. The species described here typify this situation. Tooth-form in *H. obliquidens* is unlike that of most species at present included in the genus *Haplochromis*. Yet three algalgrazing species are known, which partially bridge this morphological gap. At the opposite extreme *H. nuchisquamulatus* exhibits incipient dental adaptation only slightly removed from a generalized *Haplochromis* type.

In Lake Victoria, then, there exist several nascent supra-specific groups which are more readily identified by ecological than morphological criteria. Since conventional taxonomic characters are, so to speak, also nascent, formal recognition of these categories is impossible. I propose, therefore, to recognize their biological and evolutionary significance only by drawing attention to their existence.

Haplochromis obliquidens Hilgendorf, 1888

Chromis (Haplochromis) obliquidens Hilgendorf, 1888, S. B. Ges. naturf. Fr. Berlin, 76. Ctenochromis obliquidens, Pfeffer, 1897, Arch. f. Naturg., 63, 60. Tilapia obliquidens, Boulenger, 1898, Trans. zool. Soc., Lond., 15, 5. Hemitilapia bayoni Boulenger, 1908, Ann. Mus. Genova (3) 4, 6; Idem, 1911, Ibid. (3) 5, 69; Idem, 1915, Cat. Afr. Fish., 3, 491, fig. 340. Haplochromis nuchisquamulatus (part), Boulenger, 1915, op. cit., 290. Clinodon bayoni (Blgr.), Regan, 1920, Ann. Mag. nat. Hist. (9), 5, 33.

Haplochromis obliquidens (part), Regan, 1922, Proc. zool. Soc., Lond. 188.

The holotype of Haplochromis obliquidens could not be examined; it is amongst those specimens, once housed in the Berlin Museum, and which cannot be located at present. However, the characters noted in Hilgendorf's original description are diagnostic.

Through the courtesy of Dr. D. Guiglia (Museo Civico di Storia Naturale, Genoa) I was able to study the holotype of Hemitilapia bayoni Boulenger, and thus to confirm

Regan's synonymy of this species with H. obliquidens.

On the other hand, I cannot agree with Regan's tentative synonomy of Hemitilapia materfamilias Pellegrin, 1913, and Haplochromis obliquidens (Regan, 1922). Reexamination of H. materfamilias type specimen revealed that Pellegrin's original description is misleading, particularly in respect of the dentition, and that the species should be referred to Macropleurodus bicolor (Blgr.) (Greenwood 1956).

Description. Based on fifty-seven fishes (size range 48-89 mm. standard length) including the holotype of Hemitilapia bayoni and five specimens in the British Museum (Natural History). Three other British Museum (Nat. Hist.) specimens were examined, but are not included in the morphometric data.

Since no marked allometry with size was determined for any character examined, measurements are given for the collection as a whole, with the exception of the smallest

specimen, which is treated separately.

Depth of body 33.4-41.2, mean (M) 37.5, length of head 29.4-34.0 (M = 32.3) per cent of standard length. Dorsal profile of head and snout straight; fairly steeply sloping in most fishes but decurved in a few individuals. Preorbital depth 12.5-17.4 (M = 15.2) per cent of head length; least interorbital width 27.8-34.7 (M = 31.8); snout as broad as or somewhat broader than long, rarely longer than broad, its length 26.6-33.3 (M = 29.2) per cent head length. Eye 29.1-33.3 (M = $31\cdot4)$; depth of cheek $19\cdot0-25\cdot0$ ($M=21\cdot5$) per cent head length.

Caudal peduncle about 11 times as long as deep; 13.2-16.4 (M = 15.0) per cent

of standard length.

Corresponding ratios for the smallest individual (48 mm. S. L.)—not included in the mean values given above—are: Head 32.3; preorbital 11.1; interorbital 27.8;

snout 27.8; eye 27.8; cheek 16.7; and caudal peduncle 16.6 per cent.

Mouth short and horizontal or very slightly oblique; posterior maxillary tip extending to the vertical from the anterior orbital margin, or almost so. Jaws equal anteriorly, the lower 31.6-41.6 (M = 37.2) per cent of head length; its length/ breadth ratio from I·I-I·7 (mode I·4).

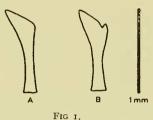
Gill rakers short; 8 or 9, rarely 7 or 10, on the lower limb of the anterior arch.

Scales ctenoid; lateral line interrupted, with 30 (f.6), 31 (f.31) or 32 (f.18) scales. Cheek with 3 (rarely 2 or 4) series of imbricating scales. 5 or 6 scales between the dorsal fin origin and the lateral line; 5-7 between pectoral and pelvic fin insertions.

Fins. Dorsal with 24 (f.25), 25 (f. 31) or 26 (f.1) rays, anal 10 (f.1), 11 (f.11), 12 (f.43) or 13 (f.2), comprising XIV-XVI, 8-10 and III, 7-10 spines and soft rays for the fins respectively. First pelvic ray slightly produced and variable in its posterior extension, usually reaching the spinous anal fin in adults and occasionally to the soft part in ripe males. Caudal sub-truncate.

ZOOL, 4, 5.

Teeth. Teeth forming the outer series are movably implanted and have slender necks with undivided, expanded, compressed and obliquely truncate crowns (Text-fig. 1). In many specimens a few postero-lateral teeth in both jaws are bicuspid but otherwise retain almost the same crown form as the more anterior teeth; in some the second cusp is incipient, but in others it is clearly differentiated. There is no correlation between length of fish and the presence or number of undifferentiated postero-lateral teeth.



A weak positive correlation exists between the number of teeth in the outer series of the upper jaw, and standard length.

S.L. (mm	ι.)		48	55-64	65-74	75-87
Tooth nu	mber		50	42-60	50-70	58-70
Mean			50	54	59	64
N			I	20	21	12

The inner teeth are mostly tricuspid and arranged in 2-4 rows, with a distinct interspace separating them from the outer series. Some obtusely tricuspid teeth, and others differing only in their smaller size from those in the outer series, frequently occur in the first inner row. These obliquely truncate teeth are larger than their tricuspid associates.

Alizarin preparations of two larvae (10 and 11 mm. total length) obtained from the mouth of a brooding female, show larval dentition to be comparable with that of *H. macrops* (Blgr.) *H. prodromus* Trewavas and *Macropleurodus bicolor* at an equivalent developmental stage. The teeth of *H. obliquidens* larvae differ considerably from the adult condition, being slender and setiform, with slightly recurved unicuspid crowns; 14–16 onter teeth, aggregated medially, are present in the upper jaw.

In certain fishes from Kisumu, it was noticed that the crowns of all teeth were coarse and irregular, and that their typical golden-brown coloration was replaced by black. Similar structural differences and discoloration have been observed in specimens of *H. michaeli* Trewavas from various localities. The cause of this aberrancy is unknown.

Lower pharyngeal bone sub-equilaterally triangular, its dentigerous surface broader than long. The numerous teeth are fine, compressed and directed posteriorly, and have truncated crowns; a small anterior cusp is present in all.

Skeleton. Differs in no important respect from that of generalized Haplochromis species. Vertebrae: 14 + 17, 13 + 17, 13 + 16 or 12 + 17.

Coloration in life: Breeding males. Ground colour bright yellow-green, becoming yellower ventrally; chest and branchiostegal membrane blackish; lips slightly irridescent. Dorsal fin yellow-grey, lappets red; orange-red spots and streaks on the posterior spinous and entire soft parts. Anal with a pinkish flush; 3 or 4 yellow ocelli. Pelvics with black outer and clear or faint pink inner half. Non-breeding adult males are similarly coloured except that the body is more nearly olivaceous and the chest not darkened. Females and juveniles of both sexes. Ground colour silvery-yellow. Dorsal and caudal fins neutral; anal and pelvic fins pale yellow. Darker, almost olivaceous females are known.

Transverse banding occurs in both sexes, but is rarely apparent in life.

Preserved material: Adult males. Dusky, the vertical bars partly or completely obscured. Dorsal fin sooty, lappets black, the posterior spinous and entire soft part maculate; anal colourless; pelvics dark laterally, pale mesially; caudal maculate. Females and juveniles. Grey to brown, with or without six to ten narrow transverse bars on the flanks; less frequently a faint mid-lateral stripe and a fainter stripe approximately following the upper lateral line. Fins colourless and immaculate.

Distribution. Haplochromis obliquidens has been collected from many localities in Lake Victoria. It is also known from the Victoria Nile.

Recently, Miss R. H. Lowe obtained a small sample of *H. obliquidens* from Lake Bunyoni (Uganda). Earlier reports (Worthington, 1932) indicated the probability that no *Haplochromis* were then present in this lake. It is presumed that those now occurring there were accidentally introduced on occasions when the lake has been stocked with *Tilapia* species; that one of the two species now recorded is probably *H. nigripinnis* Regan (otherwise endemic to Lake Edward) and the other is *H. obliquidens* supports this assumption, since *Tilapia* have been introduced from both Lakes Edward and Victoria.

The nine Lake Bunyoni H. obliquidens (size range 63–85 mm. S.L.) differ slightly from the Lake Victoria population in the following characters: body more slender, $30\cdot2-34\cdot5$ ($M=32\cdot4$) per cent of standard length; the preserved coloration of sexually mature males is apparently more melanic; in three specimens the outer series of teeth is entirely composed of bicuspids similar to the undifferentiated postero-lateral teeth of Lake Victoria fishes. In all other observed morphological characters the two populations are identical.

Ecology: Habitat. Shallow littoral zone, particularly in the vicinity of emergent vegetation; less commonly in the water-lily zone, over exposed sandy beaches and at the margin of papyrus swamps. There are indications, both from fishing and direct observation, that H. obliquidens may frequent rocky shore-lines, where the substrate is largely composed of broken rocks and boulders. The species has often been collected and seen around rock foundations of piers.

Food. The intestine of H. obliquidens is long and much coiled ($2\frac{1}{2}$ -3 times S.L.); stomach large and distensible. Stomach and intestinal contents of fifty-three individuals (size range 48-89 mm. S.L.) from various localities, have been examined.

Diatoms comprised the main digested contents in forty-four individuals; the

genera principally recorded were: Melosira, Suririella, Gomphonema, Rhopalodia, Navicula and Cyclotella.

Small fragments of plant epidermis occurred in the stomachs of twenty-nine fishes. The quantity ingested by individuals varied considerably. It was observed that, unless ruptured, most epidermal cells were apparently undigested.

Blue-green algae, especially *Rivularia* and *Microcystis*, and less frequently *Anabaena* and *Oscillatoria*, were recorded from nineteen stomachs; none of these plants showed signs of digestion.

Filamentous green algae, chiefly *Spirogyra* and to a lesser extent *Oedogonium*, occurred in sixteen stomachs. No digestion was noted.

The stomach contents of one individual comprised only partly digested fragments of Ephemeroptera larvae, probably taken at the time of their emergence. Fragmentary remains of both adult and larval insects were found in the intestines of three other fishes.

The frequent occurrence of epiphytic algae and epidermal fragments of phanerogams suggests that *H. obliquidens* feeds partly by scraping the surface of submerged leaves and stems. This supposition is confirmed by observations made on the feeding behaviour of these fishes in the lake; the peculiar dentition of *H. obliquidens* would seem to be highly adapted for such habits.

On the other hand, sand grains and bottom debris were also found in many stomachs; indeed, it was often difficult to determine whether ingested plant fragments were the partly digested remains of epidermis scraped from living plants or whether they were derived from the semi-decayed debris which accumulates near dense plant stands. Probably *H. obliquidens* feeds both by grazing on plants and by utilizing plant material contained in the bottom detritus. In either eventuality it is clear that diatoms are the principal food organisms utilized, and that much ingested plant material is voided undigested.

Although rather infrequent, the occurrence of insects in the pabulum could indicate that the species is partly facultative in its feeding habits and may utilize temporary and seasonal abundances of animal food.

Breeding. Breeding behaviour and spawning sites of *H. obliquidens* are unknown. However, females carrying young in the buccal cavity have been obtained from most localities.

The smallest sexually active fish was a female 61 mm. long; above 68 mm. S.L., most individuals were found to be mature.

Affinities and taxonomic status of the species

Particular interest attaches to *H. obliquidens*, since although it is the type species of the genus its dental morphology is unique amongst the very numerous species of *Haplochromis*. Throughout this discussion the generic diagnosis is taken to be that prepared by Regan (1920) in which particular emphasis was laid on neurocranial osteology. Subsequently this definition has been modified by the recognition of several related genera distinguished from *Haplochromis* by their divergent dentition (Regan, 1922; Trewavas, 1938; Greenwood, 1956).

Within the genus thus defined two types of outer teeth predominate, a unicuspid, conical form and a bicuspid compressed type. The common dental pattern is a single outer series distinctly separated from the inner series, usually comprising two or three rows anteriorly and a single row postero-laterally.

Tooth form and pattern have played an important part in species discrimination and in the actual or attempted delimitation of supra-specific groups amongst Lake Victoria species. Extreme dental specialization, associated with osteological changes, characterises four of the five monotypic cichlid genera in this lake (Regan, 1922; Greenwood, 1956), whilst less obvious dental characters were used in an attempt to subdivide the endemic *Haplochromis* into five genera (Regan, 1920). Two years later, Regan abandoned this concept, reducing some of his genera to subgeneric rank and discarding others (*idem*, 1922).

Because the dental morphology of *H. obliquidens* does not conform with that usual for *Haplochromis*, there might appear to be grounds, as Regan suggested (op. cit.), for recognizing at least one sub-genus to accommodate those species with unequally bicuspid or conical outer teeth. The sub-genus *Ctenochromis* (Pfeffer, 1893) would be available for such species (Regan, loc. cit.). In that paper Regan first indicated *H. astatodon* Regan of Lake Kivu as providing a dental type, which although invariably bicuspid, linked the "obliquidens" tooth form with that of the commonly occurring *Ctenochromis* type. The teeth of *H. astatodon* exhibit some diversity in the degree to which they approach the "obliquidens" condition, but the greatest number of individuals has teeth approximating more closely to this type than to "Ctenochromis". The common tooth form in *H. astatodon* may be likened to a bicuspid variant of typical *H. obliquidens* teeth; indeed, similar teeth frequently occur postero-laterally in both jaws of *H. obliquidens*.

Two other annectent species have since been found: *H. annectidens* Trewavas from Lake Nabugabo and a new species (described below) from Lake Victoria. Intra-specific variation in the tooth form of this latter species is as great as that of *H. astatodon*, but most individuals possess teeth similar to the undifferentiated postero-lateral teeth of *H. obliquidens*.

It is clear, then, that although the teeth of *H. obliquidens* may represent an extreme form, intermediates linking them to the usual bicuspid *Haplochromis* type are found as the characteristic dentition in three extant species. The gap separating the most "obliquidens"-like teeth of *H. astatodon* and the new species from those of *H. obliquidens* is relatively slight; it represents no more than the loss of a small cusp from an expansive, compressed and obliquely truncate crown. Less modified crown structure as seen in some teeth of these two species, grades through the condition found in *H. nuchisquamulatus*, into the more usual, acutely bicuspid form.

Thus, the case for recognizing at least two sub-genera of *Haplochromis* on the basis of dental morphology (Regan, 1920 and 1922) is weakened. As was mentioned earlier, several ecologically defined groups, each comprising apparently related species, are known from Lake Victoria. In every case, the group shows certain morphological divergence from the generalized *Haplochromis* type, but no clear-cut gap has evolved which would allow for its formal recognition as a sub-genus.

Study material and distribution records

	Museu	m and	Reg. 1	No.		Locality.		Collector.
				Hemitilapia 10.19.6 (pa		Sesse Islands		Bayon.
of H .	bayoni)					Sesse Islands		Bayon.
British	Museum	(N.H.)	1911,	3.3.80		Jinja (Ripon Falls)		Bayon.
British	Museum	(N.H.)	1913,	9.30.13-18		Lake Victoria		Bayon.
British	Museum	(N.H.)	1956,	7.9.1-16		Jinja (Pier)		E.A.F.R.O.
,,	11	,,	,,	,, ,, 17-20		Beach near Nasu Point		11
						(Buvuma Channel)		
,,	,,	",	,,	,, ,, 21-27		Grant Bay (Buvuma Channel)	•	11
**	,,	21	,,	,, ,, 28		Napoleon Gulf, near Bugungu (opp. Jinja)	٠	,,
>>	,,	,,	,,	,, ,, 29-32		Entebbe Harbour		,,
21	1>	2 >	,,	,, ,, 33-45		Kisumu, Kavirondo Gulf		,,
,,	,,	,,	,,	,, ,, 46-55		Mwanza, Capri Bay		**
27	>=	,,	11	,, ,, 56-57		Godziba Island		,,
27	,,	22	,,	,, ,, 169-17	0 .	Kalagala, Victoria Nile		11

Haplochromis lividus sp. nov.

Haplochromis nuchisquamulatus (part), Blgr., 1915, Cat. Afr. Fish., 3, 290, Fig. 197. Haplochromis desfontainesii (part), Blgr., 1915, op. cit., 302. Haplochromis nubilus (part), Regan, 1922, Proc. zool. Soc., London, 164.

Type specimen. A male 90 + 21 mm. from Bugungu (near Jinja), Uganda.

Description. Based on seventy-seven fishes (size range 46–90 mm. S.L.) from Lake Victoria. Five specimens from Lake Kyoga are considered separately.

Within the size range of individuals studied no character showed marked allometry with standard length or length of head; measurements are therefore given for the whole collection with the exception of the smallest fish, which was not included when determining means.

Depth of body $33\cdot3-41\cdot2$ (M = $36\cdot5$); length of head $31\cdot0-35\cdot0$ (M = $32\cdot7$) per cent of standard length. Dorsal head profile straight and moderately steeply sloping (ca. 45°), rarely somewhat curved. Preorbital depth $12\cdot0-16\cdot7$ (M = $14\cdot7$) per cent head length; least interorbital width $26\cdot2-33\cdot3$ (M = $29\cdot7$); snout as broad as long, its length $26\cdot0-32\cdot0$ (M = $28\cdot8$) per cent of head. Eye $28\cdot0-36\cdot0$ (M = $31\cdot4$); depth of cheek $17\cdot0-24\cdot1$ (M = $20\cdot1$) per cent head length.

Caudal peduncle $1 \cdot 1 - 1 \cdot 7$ (M = $1 \cdot 4$) times as long as deep; $12 \cdot 2 - 18 \cdot 5$ (M = $15 \cdot 5$) per cent standard length.

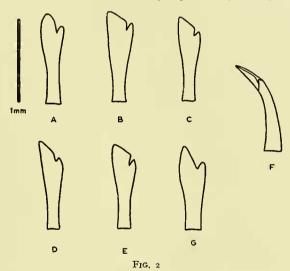
Corresponding ratios for the smallest fish (46 mm. S.L.) are: Depth 39.0, head 39.0 per cent of standard length. Preorbital 12.8, interorbital 23.2, snout 27.8 and cheek 16.7 per cent of head-length. Caudal peduncle 15.2 per cent of S.L.

Mouth horizontal or slightly oblique; posterior maxillary tip reaching the vertical to the anterior orbital margin or nearly so, and to the eye in some. Lips slightly thickened. Lower jaw $33\cdot3-41\cdot0$ (M = $37\cdot2$) per cent of head, its length/breadth ratio $1\cdot3-2\cdot0$ (mode $1\cdot6$).

Gill rakers short, 8 or 9 (less frequently 7 or 10) on the lower part of the first arch. Scales ctenoid, lateral-line interrupted, with 30 (f.7), 31 (f.16), 32 (f.48), 33 (f.5), or 34 (f.1) scales. Cheek with 2 or 3 (rarely 4) series. 5 or 6 scales between dorsal fin origin and the lateral line; 5 or 6 between pectoral and pelvic fin insertions.

Fins. Dorsal with 23 (f.1), 24 (f.34), 25 (f.40) or 26 (f.2); anal II (f.18), I2 (f.55), and I3 (f.4), rays, comprising XV-XVI 8-10 and III, 8-10 spinous and soft rays for the fins respectively. First pelvic ray produced, variable in its posterior extension, but reaching the spinous anal in most adults. Pectoral fins as long as, or slightly shorter than the head. Caudal sub-truncate.

Teeth. In the form and pattern of its teeth, H. lividus departs from the generality of Haplochromis species. The anterior and antero-lateral teeth in the outer series are movably implanted and have slender necks (somewhat stouter than in H. obliquidens) with compressed, expanded and obliquely truncated, unequally bicuspid crowns. The posterior cusp shows some variation in size, but it is always smaller than the anterior, from which it is narrowly separated (Text-fig. 2). It should be



noted that these teeth bear a striking resemblance to the undifferentiated posterolateral teeth of *H. obliquidens*. Posterolateral teeth in *H. lividus* are either similar to the anterior teeth or indistinguishable from the generalized acutely bicuspid type (Text-fig. 2G). Less frequently, unicuspid teeth occur in this position. A weak positive correlation exists between the number of teeth in the outer series of the upper jaw and standard length.

S.L. (n	ım)			46		E6_6E		66.75		76-85		06
D (11		•	•	40	•	30-03	•	00-75	•	70-05	•	oo-91
Tooth	numb	oer		36		42-58		38-66		44-75		52-66
Mean	•	•	•	36		50		54		61		57
N				1		8		27		33		5

Teeth forming the inner rows are invariably tricuspid and small. No obtusely cuspidate teeth, or teeth similar to those of the outer series, have been observed (cf. H. obliquidens in which such teeth are frequently encountered).

There is considerable variation in the number and disposition of inner rows. From 2-5 and from 2-4 series occur in the upper and lower jaws; individuals with more than three rows usually have the interspace between outer and inner teeth greatly reduced or even absent, particularly in the upper jaw.

Lower pharyngeal bone sub-equilaterally triangular; dentigerous surface slightly broader than long. Pharyngeal teeth similar to those described for H. obliquidens. Osteology. That of a typical generalized Haplochromis species; vertebrae 14 + 16 (in two specimens).

Coloration. Breeding colours of male *H. lividus* are perhaps the most distinctive morphological characteristic of the species and are not repeated or even approached in any other Lake Victoria *Haplochromis*. In preserved material their brilliance is lost. Sexually active males. Ground colour light olive-green shading to slate-grey ventrally; flanks (including the dorsal aspects and in some, the nape) with a goldenred flush extending from the head to the caudal peduncle origin. Inter-orbital region of the head, the snout, lips and preorbital with a vivid, almost fluorescent, blue sheen, traces of which often extend onto the otherwise slate-grey lower jaw, lower preopercular limbs and the branchiostegal membrane. As far as can be determined, the intensity of this peculiarly intense head coloration is little influenced by the fishes' emotional state. On the other hand, its greatest extension is apparently manifest only in breeding fishes.

Dorsal fin grey to sooty, slight indications of fluorescent blue can be detected in some individuals; red streaks on the posterior spinous and entire soft part; lappets orange-red. Caudal dark, with ill-defined red maculae concentrated proximally on the upper half. Anal dark, with 2–4 yellow ocelli. Pelvics black, becoming lighter on the medial third. Coloration of *immature males* is similar except that the blue head colour is less concentrated and intense, or it may even be absent. The flanks are also less intensely red. *Females*. Ground colour light grey-green, becoming silver ventrally. Dorsal, caudal and pectoral fins colourless or faintly yellow-grey. Anal and pelvic fins yellow.

Preserved material: Males. Ground colour variable, usually grey. Dorsal caudal and anal fins clear or dark, the two former maculate as in life; pelvics black. The blue head coloration is lost, but in most individuals it is faintly represented by a dead-white or ashen colour (at least in formalin fixed material preserved in spirit for five years). Females and immature males. Ground colour as above. All fins clear. From 5-7 transverse bars on the flanks; the posterior pair rarely extend below the level of the lower lateral-line and are often joined by a short longitudinal stripe. Faint indications of a mid-lateral stripe are present in some individuals. Banding and striping are sometimes apparent in living fishes, but are intensified after death.

Distribution. H. lividus is known from several localities in Lake Victoria. (See below.)

Ecology: Habitat. Shallow littoral zone, especially in the vicinity of emergent and submerged vegetation, less frequently in the water-lily zone and at the margin

of papyrus swamps; the species is commonly encountered over rock foundations of piers. Thus, the habitat preferences of *H. lividus* are similar to those of *H. obliquidens* with which species it is usually captured. There are, however, indications that *H. lividus* may inhabit the deeper littoral zone where *H. obliquidens* are relatively scarce.

Food. The intestine is long $(2-2\frac{1}{4}$ times standard length) and much coiled; the stomach large and distensible. The stomach contents of sixty-two individuals (size range 56-90 mm. S.L.) from most localities have been examined. In general the food of H. lividus is similar to that of H. obliquidens.

Diatoms of the genera *Melosira* and *Rhopalodia* comprised the predominating digested contents in the stomachs of forty-five fishes, and were significant in twelve others.

Fragments of plant epidermis were found in thirty-three stomachs; as in *H. obliquidens* the amount and fragment-size showed considerable variation.

Filamentous green-algae, represented by *Spirogyra*, were recorded from only four fishes; in none was there any indication of digestion. Blue-green algae (especially *Rivularia* and *Microcystis*) were found in twenty-four stomachs. Again, the algae were apparently not digested.

Very fragmentary animal remains (Ostracoda, Crustacea [Decapoda] and Insecta [larval Chironomidae]) were recorded from sixteen individuals.

The occurrence of Insecta (winged Hymenoptera) as the main stomach contents in twelve fishes collected contemporaneously at one station, is of particular interest. Besides insect remains, diatoms were well represented in these stomachs. This observation suggests that *H. lividus* may feed facultatively on animal food at times of local abundance. Insects also comprised the main contents of two other specimens, both from different localities.

Feeding habits of *H. lividus* are probably similar to those of *H. obliquidens*. Direct observation shows the species to be a grazer on submerged plants and stones, whilst the occurrence of sand-grains and bottom debris in some stomach contents indicates occasional benthic feeding.

Breeding. Breeding habits and sites are imperfectly known. Three females carrying young in the buccal cavity have been collected; one from an exposed beach flanked by dense emergent vegetation and two from an off-shore water-lily stand. From one of these fishes twenty-five larvae of 12 mm. total length were recovered; the other females had jettisoned the greater part of their broods.

Affinities. Disregarding for the moment its peculiar male breeding coloration, *H. lividus* shows marked affinity with *H. astatodon*, *H. annectidens* and *H. obliquidens*, especially with regard to dental characteristics. Save *H. annectidens*, for which no information is available, the food of these species is similar, and composed mainly of epiphytic algae and plant debris (Poll and Damas, 1939, for food of *H. astatodon*).

In fact, *H. lividus*, *H. astatodon* and *H. annectidens* seem to provide examples of herbivorous intermediates linking generalized and usually insectivorous *Haplochromis* species with the specialized algal-grazer, *H. obliquidens*.

Within the species flock of Lake Victoria H. lividus shows some morphological relationship with H. nuchisquamulatus. Anatomical and dental characteristics

might entitle *H. nuchisquamulatus* to consideration as the extant representative of an annectant form between *H. lividus* and the generalized species typified in Lake Victoria by *H. nubilus* (Blgr.) and *H. macrops* (Blgr.).

The present distribution of species having "lividus"-like teeth requires little comment. Haplochromis astatodon is endemic to Lake Kivu, whose Haplochromis species flock has long been recognized as having well-defined Victorian affinities (Regan, 1921), although the possibility of convergent evolution in the two lakes cannot be entirely discounted. Haplochromis annectidens is endemic to Lake Nabugabo and is part of a small species group which could only have been derived from that of Lake Victoria (Trewavas, 1933).

The presence within Lake Victoria of both *H. lividus* and its morphological derivative *H. obliquidens* is suggestive of an ancestor-descendant relationship. Before accepting this apparent phylogeny, due regard must be paid to the unique male breeding coloration of *H. lividus*. Baerends and Baerends van Roon (1950) expressed the opinion that male coloration plays an important part in species recognition amongst cichlids. Thus, we may assume the importance of male coloration as a barrier to interspecific mating. Field observations on the *Haplochromis* of Lake Victoria lend weight to this hypothesis. Although male colours and colour-patterns are broadly repeated in several species, no instance has yet been recorded of related species with identical or near identical male coloration breeding in the same habitat.

Therefore, although the distinctive coloration of *H. lividus* might be used in argument against close relationship with *H. obliquidens*, it might equally well be interpreted as resulting from selection strengthening mating barriers between species which occupy similar habitats, especially if the species are closely related and of recent origin.

Diagnosis. Haplochromis lividus differs from other Haplochromis in Lake Victoria in having distally compressed and expanded teeth whose crowns are unequally bicuspid and obliquely truncated. Dentition serves to distinguish this species from the fluviatile Haplochromis of East Africa. In life male coloration is the most obvious diagnostic character.

From species with similar dental morphology *H. lividus* may be differentiated as follows: from *H. astatodon* by its larger eye/cheek ratio; from *H. annectidens* by its slightly wider interorbital region and somewhat stouter, shorter teeth. In life coloration distinguishes *H. lividus* and *H. astatodon*; live colours are unknown for *H. annectidens*.

Five specimens from Lake Kyoga (*Tilapia nubila* B.M. (N.H.) reg. nos. 1911.3.3. 141–145; 60–66 mm. S.L.) have teeth and dental patterns of the *H. lividus* type, but differ from Lake Victoria specimens in the following characters: dorsal head profile steeper; body deeper; and greater depth of cheek (23·3–25·2, mean 24·1 per cent head length). Should further collections from Lake Kyoga show that these fishes have *H. lividus* coloration (as is suggested in the preserved material) and should they also maintain the observed differences in morphology, then it will be necessary to recognize a distinct sub-species in that lake.

Study material and distribution records

	Mus	eum and	reg	. no.			Locality.		Collector.
Briti	sh Museum	(N.H.)	190	6.5.30.3	18-320		Entebbe		Degen.
Briti	sh Museum	(N.H.)	1956	.7.9.63-	65 .		Jinja Pier		E.A.F.R.O.
,,	,,	,,	,,	,, ,, 58–	62 .		Beach near Jinja		.,
,,	,,	.,,	,,	,, ,, 66–	74 •		Napoleon Gulf, near		,,
			-	paratypes	,		Bugungu (opp. Jinja)		22
12	,,	"	,,	·· ·· 75-	83 .		Kirenia (near Jinja)		23
,,	**	11	,,	,, ,, 84-	94 •		Entebbe Harbour	•	21
,,	,,	12	,,	,, ,, 95-	99 •		Beach near Nasu Point,		**
							Buvuma Channel		,,
,,	,,	2.1	,,	,, ,, IOO	-102		Hannington Bay (Uganda) .	,,
,,	11	,,		,, ,, 103		•	Grant Bay (Uganda)		,,
"	**	,,		,, ,, 125			Mwanza, Capri Bay		",
"	"	- 11	,,	,, ,, 126	-128		Majita (Tanganyika	•	**
							Territory)		

Haplochromis nigricans (Blgr.) 1906

Tilapia nigricans (part) Blgr., 1906, Ann. Mag. nat. Hist. (7) 17, 448; Idem, 1907, Fish. Nile, 518; Idem, 1911, Ann. Mus. Genova (3) 5, 75; Idem, 1915, Cat. Afr. Fish., 3, 241, fig. 160. Tilapia simotes Blgr., 1911, Ann. Mus. Genova (3) 5, 75; Idem., 1915, op. cit., 242, fig. 161. Neochromis nigricans (Blgr.), Regan, 1920, Ann. Mag. nat. Hist. (9) 5, 33. Haplochromis (Neochromis) nigricans (Blgr.), Regan, 1922, Proc. 200l. Soc., London, 163.

As Regan (1922) first showed, Boulenger's figure of $Tilapia\ nigricans$ is misleading. It was prepared from a specimen distorted in preservation and consequently the head profile differs considerably from that of $T.\ simotes$. However, in the important characters of dental pattern and morphology both species are identical. If the head of the figured specimen is restored to its natural position the characteristically decurved profile of $Haplochromis\ nigricans$ is apparent.

Description. Based on fourty-four specimens (size range 49-94 mm. standard length) including holotypes of T. nigricans and T. simotes. Other specimens in the British Museum (Nat. Hist.) collections were examined but are not included in the morphometric data. The paratype of T. nigricans is clearly not referable to this species and should probably be placed in H. lividus. Its small size permits only tentative identification. Both skeletons in the British Museum (Nat. Hist.) are of H. nigricans.

Depth of body 34.5-40.0 (mean 36.9), length of head 28.0-33.3 (M = 31.2) per cent of standard length. Dorsal head profile strongly decurved. Preorbital depth 11.8-16.7 (M = 14.6) per cent of head length; least interorbital width 25.0-31.5 (M = 28.8); snout broader than long in most specimens of more than 65 mm. S.L., and as long as broad in smaller fishes, its length 26.3-35.2 (M = 30.4) per cent of head. Eye 25.9-33.3 (M = 30.0), depth of cheek 10.4-27.3 (M = 32.4) per cent of head.

Caudal peduncle from $1\cdot 1-1\cdot 8$ (mode $1\cdot 3$) times as long as deep, its length $11\cdot 4-17\cdot 6$ (M = $15\cdot 4$) per cent of standard length.

Mouth horizontal; posterior maxillary tip reaching the vertical from the anterior orbital margin or extending somewhat beyond. Jaws equal anteriorly, the lower short and broad, from $30\cdot0-37\cdot8$ (M = $35\cdot6$) per cent of head length, its length/breadth ratio $1\cdot0-1\cdot4$ (mode $1\cdot2$). H. simotes holotype is unusual in having its lower jaw only 28 per cent of the head length.

Gill rakers short, 8 or 9 (rarely 10) on the lower part of the first arch.

Scales ctenoid; lateral line interrupted, with 30 (f.1), 31 (f.12) 32 (f.28), or 33 (f.3) scales. Cheek with 2 or 3 (rarely 4) series of scales; 6 or 7 (less frequently 5 or $5\frac{1}{2}$) between dorsal fin origin and the lateral line; 7 or 8 (rarely 6 or 9) between pectoral and pelvic fin insertions.

Fins. Dorsal with 24 (f.7), 25 (f.33) or 26 (f.4) rays, anal 11 (f.7), 12 (f.32) or 13 (f.5), comprising XIV-XVIII, 8-10 and III, 8-10 spinous and soft rays. First pelvic ray produced, extending to the vent or even to the soft anal; its posterior extension not correlated with sex or maturity. Pectoral fin shorter than the head. Caudal sub-truncate or feebly rounded; scaled on the proximal half to two-thirds.

Teeth. The outer series is composed of close set, movably implanted bicuspid teeth, with long, slender necks and expanded crowns. Cusp size in some individuals is markedly disparate, whilst in others the cusps are sub-equal. In the upper jaw, teeth situated postero-laterally are either tri- or unicuspid.

A weak positive correlation exists between the number of teeth in the outer series of the upper jaw and standard length.

S.L. (mm.) .	49-58	59–68		69-78	79-93
Tooth number	40-50	46-60		46-60	54-70
Mean	46	52		52	62
N	19	6	٠	14	4

The inner series is composed of small tricuspid teeth; 3-7 (mode 4) rows in each jaw. Compared with other Lake Victoria *Haplochromis* (except some individuals of *H. nuchisquamulatus* and *H. lividus*) the space separating inner and outer tooth series is greatly reduced in *H. nigricans*; it is non-existent in 30 per cent of the specimens examined.

Lower pharyngeal bone sub-equilaterally triangular; dentigerous surface somewhat broader than long; teeth numerous, and similar to those in H. obliquidens and H. lividus.

Cranial skeleton. The short and strongly decurved snout is reflected in the neurocranial shape. This differs slightly from that of generalized *Haplochromis* by having a more steeply sloping ethmo-vomer complex. Also, the dentary is relatively stouter and more massive in *H. nigricans*.

Coloration in life: Breeding males. Ground colour black, shot with metallic blue; snout, lips, interorbital region and to a lesser degree, cheeks and opercula, bluish. Dorsal fin black, lappets and maculae on the soft part deep crimson; anal dusky crimson, ocelli yellow; caudal crimson, pelvics black. Adult females and juveniles. Ground colour olivaceous; a faint golden-yellow flush over the opercula and branchiostegal membrane. Dorsal and anal fins dark yellow; caudal greygreen; pelvics dusky yellow.

Preserved material: Adult males. Black or slate grey; seven or eight transverse bars visible on the flanks of light coloured fishes. Dorsal fin black, with pale margin and maculae; caudal black proximally, pale distally; anal pale; pelvics black. Females and juveniles. Ground colour greyish-brown, with seven or eight dark transverse bars on the flank; a pronounced lachrymal stripe. All fins hyaline or slightly darkened.

Particular interest attaches to a single adult female with black and yellow piebald coloration similar to that described in Macropleurodus bicolor (Blgr.) and Hoplotilapia retrodens Hilgen. (Greenwood, 1956). The significance of this atypical individual is difficult to assess. In other characters H. nigricans does not manifest any apparent relationship with the monotypic genera, nor with H. sauvagei (Pfeffer), another species exhibiting sex-limited polychromism. It is probably the result of independent but parallel mutation occurring in H. nigricans, and therefore of no phyletic value. Such a phenomenon might be expected amongst members of a recently evolved and oligophyletic species flock.

Distribution. Lake Victoria and the Victoria Nile. Although most localities represented in the present collection are in Uganda, this should not be taken to indicate that H. nigricans is confined to, or more abundant in, these waters. The species has been seen in many areas, but its lithophilic habits render capture difficult

except by unconventional or specialized gear.

Numerous specimens have been caught at Godziba Island (1° 29' S., 32° 36' E.). This small, rocky outcrop lies slightly south and west of the centre of Lake Victoria and is distant from either the mainland or other off-shore islands. Because there is no indication of H. nigricans ever occurring in deep or sub-littoral waters, one is led to suppose that Godziba fishes are at present isolated from coastal populations, and have been isolated for some considerable time. With this in mind, the Godziba sample was carefully compared with others from the mainland, but no phenotypic peculiarities could be detected.

Ecology: Habitat. H. nigricans is apparently confined to rocky and shallow areas of the littoral zone. Since rock exposures are not infrequent in the exposed littoral, its habitat, broadly speaking, overlaps that occupied by other algal-grazing Haplochromis species. No data are available for populations living in the Nile.

Food. The intestine is long (ca. 2½-3 times S.L.) and coiled. Observations on fishes in the lake indicate that H. nigricans feeds by grazing on algae from rock

surfaces, a conclusion which is supported by stomach content analyses.

Ingested material from thirty-two stomachs showed a preponderance of diatoms over all other material. Specific identification of these plants was impossible, but the genera represented (chiefly Navicula, Synedra, Rhopalodia and Gomphonema) are typically epilithic or epiphytic in Lake Victoria (Ross, 1954). The absence, except from two stomachs, of fragmentary phanerogam tissue (an important element in stomach contents of other algal grazing species) was noteworthy, but explicable if H. nigricans graze from rock surfaces.

Filamentous green algae (Spirogyra and Oedogonium) and blue-green algae occurred less frequently, and were apparently undigested.

Very fine, sand-grain-like particles were recorded from thirteen stomachs. That

these might have been fragments derived from rock surfaces and not the bottom seems likely in the absence of bottom debris typically associated with a sand substrate.

Breeding. Spawning sites are unknown. Courtship activity has been observed amongst fishes living over rocks near the Ripon Falls, but actual spawning was not seen. Two females have been found with embryos and larvae in the buccal cavity; it is assumed that *H. nigricans*, like the generality of *Haplochromis* species, is a mouth-brooder.

The smallest adult fishes recorded were a female 51 mm. and a male 55mm. in standard length. Males apparently reach a larger size than females since no female greater than 70 mm. S.L. has been captured.

Affinities. Haplochromis nigricans is closely related to H. serridens Regan of Lake Edward (vide Trewavas, 1933). Both species have almost identical dental morphology and pattern, as well as similarity in general facies and preserved coloration. No clear-cut quantitative characters can be found to separate the species. There is, however, a subtle difference in their gross morphology, probably attributable to the more rounded physiognomy of H. serridens. Also, the inner tooth bands of this species are usually broader and possess more teeth than those of H. nigricans.

Tooth form, and less obviously the dental pattern, in one other Lake Edward species, *H. fuscus* Regan, is similar to that of *H. nigricans*; but the species are readily distinguished by the smaller nuchal and thoracic scales in *H. fuscus* and also by its thicker lips and more abruptly declivous dorsal head profile.

Amongst Lake Victoria species H. nigricans is probably related to, and derived from a species resembling H. nuchisquamulatus.

Diagnosis. H. nigricans is distinguished from other Lake Victoria Haplochromis with bicuspid outer teeth by the following combination of characters: a short and broad lower jaw (modal length/breadth ratio I:2); slender, movably implanted outer teeth narrowly separated, if at all, from the broad bands of inner teeth; a strongly decurved dorsal head profile; a long and convoluted intestine.

Study material and distribution records

British Museum (N.H.) 1906.5.30.469 (Holotype of Tilapia nigricans) Entebbe . Degen. Genoa Museum (Holotype of Tilapia simotes) . Kakindu (Victoria Nile) . Bayon. British Museum (N.H.) 1911.3.3.160–163 (Para-	
Genoa Museum (Holotype of Tilapia simotes) . Kakindu (Victoria Nile) . Bayon.	
71 71 7	
British Museum (N.H.) 1011 2 2 160-162 (Para-	
Ditton bidsedin (1.11.) 1911.3.3.100-103 (1 dfa-	
types of T. simotes) Jinja (Ripon Falls) . Bayon	
British Museum (N.H.) 1911.3.3.156-158, plus	
one additional specimen (Paratypes of T. simotes) Kakindu Bayon	
British Museum (N.H.) 1956.7.9.129-136 . Napoleon Gulf, near . E.A.F.R.C).
Ripon Falls	
,, ,, ,, ,, ,, 137–148 . Jinja Pier . ,,	
,, ,, ,, ,, ,, 149–150 . Napoleon Gulf, near . ,,	
Jinja	
,, ,, ,, ,, ,, ,, 151 . Beach near Nasu Point, . ,,	
Buvuma Chanuel	
,, ,, ,, ,, 152 Buka Bay (Uganda) . ,,	
,, , ,, ,, 153–165 . Godziba Island . ,,	

Haplochromis nuchisquamulatus (Hilgendorf) 1888

Chromis nuchisquamulatus Hilgend., 1888, S. B. Ges. naturf. Fr. Berlin, 76.
Ctenochromis nuchisquamulatus (Hilgend.), Pfeffer, 1896, Thierw. O. Afr. Fische, 14.
Tilapia nigricans (part), Blgr., 1915, Cat. Afr. Fish., 3, 241.
Haplochromis nuchisquamulatus (part), idem, ibid., 290.
Haplochromis (Neochromis) nuchisquamulatus (Hilgend.), Regan, 1922, Proc. zool. Soc., London,

Haplochromis (Neochromis) nuchisquamulatus (Hilgend.), Regan, 1922, Proc. zool. Soc., London, 163.

The holotype of *H. nuchisquamulatus* is amongst those specimens, once housed in the Berlin Museum, which cannot be located at the present time. It is thus the more regrettable that Hilgendorf's original description is totally inadequate for modern

taxonomic purposes.

As a basis for comparison I have therefore relied upon Regan's identification of two British Museum (Nat. Hist.) specimens. From Regan's paper (1922) it is clear that he, too, was unable to study the type specimen, but he apparently gained sufficient information from photographs and data supplied by Dr. Pappenheim to identify his material. Of this I have located only one specimen (British Museum (N.H.) reg. no. 1911.3.3.155, from Kakindu, Victoria Nile). In its general morphology this fish agrees closely with a photograph of the type. Further, with the aid of a binocular microscope it has proved possible to check certain other characters visible in this remarkably clear photograph.¹

Although this species is represented in my study-material by only six specimens, I have little doubt as to its biological validity. Morphologically H. nuchisquamulatus is intermediate between H. lividus and H. nigricans: it may well represent the stock from which these species diverged. The tooth form of H. nuchisquamulatus is less specialized than that of H. lividus and is nearer H. nigricans. That is to say, the outer teeth are slender, bicuspid and movable, whilst those of the inner series show a tendency towards an increase in the number of rows and a decrease in the space separating them from the outer series. The lower jaw is more slender than in H. nigricans and is similar to the dentary in H. lividus and H. obliquidens, and in other, more generalized Haplochromis.

None of the dental and associated characters considered above lies within the known range of intra-specific variability for *H. nigricans* or *H. lividus*. Neither is there any indication by analogy with well-defined *Haplochromis* species that the "nuchisquamulatus" character-complex is an extreme variant of some other species

Description. The principal morphometric characters for each of the six specimens examined are tabulated below. All are adult males.

S.L.	Depth.*	Head.*	Po. %	Io. %	Snt. %	Eye. %	Ch. %	Lj. %	C.P.*
83.0	38·o	31.3	15.4	30.8	30.8	30.8	23.0	36.5	15.7
86·o	37.2	32.5	14.3	28.6	28.6	32.2	23.2	35.7	15.2
93.0	38.7	32.3	14.5	29.0	32.2	29.0	24.2	38.6	15.1
98.0	38.8	31.6	16.2	30.0	32.2	25.8	22.6	38.7	15.3
99.0	37.4	32.8	15.4	30.8	30.8	30.8	24.6	40.0	15.2
113.0	37.0	30.3	17.4	26.5	31.8	29.0	26.5	36.2	18.6

^{*} Percentage standard length. % Percentage head-length.

¹ To be reproduced in a later part of this series.

Dorsal head profile curved and sloping. Mouth horizontal; posterior maxillary tip extending to the vertical from the anterior orbital margin or slightly beyond. Jaws equal anteriorly, the length/breadth ratio of the lower 1·4-1·7 (mode 1·5).

Teeth. Outer teeth unequally bicuspid; a few slender and unicuspid teeth occur posteriorly in the upper jaw, in which there are from 50-70 teeth. Although relatively fine, the neck in these teeth is stouter and less clearly demarcated from the expanded crown, than in H. lividus or H. obliquidens.

Inner teeth small and tricuspid, occurring in 4-8 and 3-6 rows in the upper and lower jaws respectively; the space separating inner and outer series is reduced.

Lower pharyngeal bone sub-equilaterally triangular, its dentigerous surface slightly broader than long. Teeth fine and numerous; in the three larger specimens, the median teeth are enlarged.

Gill rakers short, 8-10 on the lower part of the first arch.

Scales ctenoid: lateral line interrupted, with 31 (f.2), 32 (f.2) or 33 (f.2) scales. Cheek with 2 or 3 series. 6-8 scales between dorsal fin origin and the lateral line; 6-8 scales between pectoral and pelvic fin insertions.

Fins. Dorsal with 24 (f.1), 25 (f.2) or 26 (f.3) rays, anal 12 (f.4) or 13 (f.2), comprising XV-XVII, 9 or 10 and III, 9 or 10 spinous and soft rays. First pelvic ray produced, extending to the second anal ray. Pectoral fins slightly shorter than the head. Caudal sub-truncate.

Skeleton. That of a generalized Haplochromis.

Coloration. Unknown in life and known only for preserved males. Ground colour dark greyish-brown, the dorsal and ventral surfaces darker than the flanks, across which seven transverse bars are visible; in two specimens the chest is black. Well-defined, narrow lachrymal and two interorbital stripes; two broad bands across the nape, one immediately post-ocular in position, the other slightly more posterior.

Ecology. Of the six specimens studied, five were caught in exposed littoral zones of Lake Victoria, and one in the Victoria Nile. The type specimen is from Lake Victoria, but no precise locality is given.

Food. Fragments of plant tissue and numerous epiphytic algae were recorded from four of the five stomachs examined, whilst the fifth contained filaments of Oedogonium and some fragmentary plant tissue.

Diagnosis. H. nuchisquamulatus is distinguished from other Lake Victoria Haplochromis with bicuspid outer teeth by the following combination of characters: long and convoluted intestine (ca. $3 \times S.L.$); relatively slender, movably implanted and numerous outer teeth; increased number of inner tooth rows (3–8) narrowly separated from the outer series. From H. nigricans it is recognized by the narrower lower jaw and less strongly decurved dorsal head profile; outer teeth in H. nuchisquamulatus are also somewhat stouter than those of H. nigricans. These acutely cuspidate teeth serve to separate H. nuchisquamulatus from H. lividus.

The diagnostic character used by Hilgendorf (small nuchal scales whose exposed surface is less than half that of flank scales) cannot be considered valid. In most *Haplochromis* nuchal scales are smaller than those on the flank, and furthermore are subject to quite considerable intra-specific size-variation.

Study material and distribution records

	Museu	m and	reg. 1	10.		Locality.		Collector.
British	Museum	(N.H.)	190	1.3.3.154 5.5.30.316	-317 .	Kakindu (Victoria Nile) Entebbe	•	Bayon. Degen.
British	Museum	(N.H.)	1956	5.7.9.166-	167 .	Beach near Nasu Point,		Degen.
						Buvuma Channel		E.A.F.R.O.
33	**	11	,,,	,, ,, 168		Godziba Island		E.A.F.R.O.

SUMMARY

- I. The algal-grazing species *Haplochromis obliquidens* Hilgendorf 1888, *H. nigricans* (Boulenger) 1906, and *H. nuchisquamulatus* (Hilgendorf) 1888, are redescribed on the basis of new and more extensive collections.
 - 2. A new species, H. lividus, apparently related to H. obliquidens is described.
 - 3. Data on the food and ecology of these species are given.
- 4. Consideration is given to the possibility of recognizing a number of supraspecific groups of *Haplochromis* in Lake Victoria. At present, although such groups may be determined, it is impossible to give them formal taxonomic status.

ACKNOWLEDGMENTS

I wish to acknowledge my gratitude and thanks to the Trustees of the British Museum (Natural History) for facilities afforded me during the tenure of a Colonial Fisheries Research Studentship; to Professor L. Bertin of the Muséum National d'Histoire naturelle, Paris, for allowing me to study type specimens of Lake Victoria Cichlidae described by Pellegrin; to Dr. Delfa Guiglia of the Museo Civico di Storia Naturale, Genoa, for the courtesies mentioned in the text; to my colleague Dr. Philip S. Corbet for identifying some of the material from gut contents; and to Mr. Denys W. Tucker, for his very helpful criticism of the manuscript. I am especially indebted to Dr. Ethelwynn Trewavas for much helpful information and advice.

REFERENCES

(Other than those given in full in the text)

- BAERENDS, G. P. & BAERENDS VAN ROON, J. M. 1950. An introduction to the study of the ethology of cichlid fishes. *Behaviour*, Supplement 1, pp. 1-242. Leiden.
- Greenwood, P. H. 1951. Evolution of the African cichlid fishes; the *Haplochromis* species flock in Lake Victoria. Nature, London, 167:19.
- --- 1956. The monotypic genera of cichlid fishes in Lake Victoria. Bull. Br. Mus. nat. Hist., Zool. 3, no. 7.
- Pfeffer, G. 1893. Ostafrikanische Fische gesammelt von Herrn Dr. F. Stuhlmann. Jahrb. Hamburg. wiss. Anst. 10 (2), 129-177, 3 pls. (1-49 sep. pag.).
- Poll, M. & Damas, H. 1939. Poissons. Exploration du Parc National Albert, mission H. Damas (1935–1936), fasc. 6, pp. 1-73.
- REGAN, C. T. 1920. The classification of the fishes of the family Cichlidae. 1. The Tangan-yika genera. Ann. Mag. nat. Hist. (9) 5:33.

REGAN, C. T. 1921. The cichlid fishes of Lakes Albert Edward and Kivn. Ann. Mag. nat. Hist. (9) 8:632.

- 1922. The cichlid fishes of Lake Victoria. Proc. zool. Soc. Lond. 157.

Ross, R. 1954. The algae of the East African Great Lakes. Proc. International Assoc.: Theoretical and Applied Limnology.

Trewavas, E. 1933. Scientific results of the Cambridge expedition to the East African lakes, 1930-1. II. The cichlid fishes. J. Linn. Soc. (Zool.) 38: 309.

— 1935. A synopsis of the cichlid fishes of Lake Nyasa. Ann. Mag. nat. Hist. (10) 16:65. WORTHINGTON, E. B. 1932. A Report on the Fisheries of Uganda. Crown Agents, London.

